

Forest plant community changes during 1989–2007 in response to climate warming in the Jura Mountains (France and Switzerland)

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Abstract

Question: How strong are climate warming-driven changes within mid-elevation forest communities? Observations of plant community change within temperate mountain forest ecosystems in response to recent warming are scarce in comparison to high-elevation alpine and nival ecosystems, perhaps reflecting the confounding influence of forest stand dynamics.

Location: Jura Mountains (France and Switzerland).

Methods: We assessed changes in plant community composition by surveying 154 *Abies alba* forest vegetation relevés (550–1,350 m a.s.l.) in 1989 and 2007. Over this period, temperatures increased while precipitation did not change. Correspondence analysis (CA) and ecological indicator values were used to measure changes in plant community composition. Relevés in even- and uneven-aged stands were analysed separately to determine the influence of forest stand dynamics. We also analysed changes in species distribution to detect shifts along the elevation gradient by focusing on the lowest, central and highest positions of lowland and mountain species altitudinal ranges.

Results: We found significant shifts along the first CA axis, which reflected a change in plant community composition towards a greater frequency of lowland species. Analyses of ecological indicator values indicated increases in temperature and light

availability in *A. alba* stands, particularly in even-aged stands. However, no major changes in overall species distribution were found.

Conclusions: The community-level changes are consistent with effects of climate warming and local stand dynamics. Changes in species distribution were small in comparison to observed local temperature increases, perhaps reflecting dispersal limitation, phenotypic plasticity or microclimatic buffering by the tree canopy. Causality cannot rigorously be inferred from such a descriptive study; however, we suggest that recent warming is now driving plant community change in the climatically more moderate mid-elevation forest setting.

Keywords: Biotic impacts; Forest ecosystems; Global warming; Plant community ecology; Range shifts; Species distribution; Vegetation change.

Nomenclature: Flora Europaea, Tutin et al. (2001).

Introduction

Mountains harbour much of the Earth's biodiversity, but their ecosystems are considered particularly vulnerable to the negative impacts of global warming (Fischlin et al. 2007). A recent bioclimatic envelope study of 1,350 European plant species concluded that species from mountains may be disproportionately sensitive to climate change, and southern mountain regions in Europe are predicted to experience particularly severe species losses (Thuiller et al. 2005). Other modelling studies have predicted the upslope retraction of nival species, with concurrent expansion of alpine species at the alpine–nival ecotone (Gottfried et al. 1999) and an upslope shift of the tree line at the subalpine–alpine ecotone (Dirnbock et al. 2003). An increasing number of studies provide support for these predictions and report observed altitudinal range shifts for mountain plant species, in particular in alpine and nival ecosystems (Klanderud & Birks 2003; Lesica & McCune 2004; Walther et al. 2005; Pauli et al. 2007; Parolo & Rossi 2008; Vittoz et al. 2008; Erschbamer et al. 2009).

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However, it is unclear to what extent such climate warming-driven changes can be generalized to mid- and low-elevation mountain ecosystems, as observations of climate warming impacts in these ecosystems are scarce (Peñuelas & Boada 2003; Kelly & Goulden 2008; Lenoir et al. 2008). Lenoir et al. (2008) reported upward shifts in optimum elevation for 171 plant species within French mountain forests. However, climate warming impacts were much less evident in several other more local studies (Walther & Grundmann 2001; Vittoz et al. 2009). Outside Europe, strong warming-related plant community changes were reported for an eastern North American temperate forest landscape (Willis et al. 2008). One of the complications for discerning climate warming-driven changes in plant community composition at lower elevations, especially in densely populated and managed areas such as Europe, is that other anthropogenic factors may also cause strong changes. Such factors include changes in forest stand structure due to forestry practices (or natural disturbances) and soil chemical changes through eutrophication and/or acidification (Falkengren-Grerup 1986; Thimonier et al. 1994; Brunet et al. 1998; Nygaard & Odegaard 1999; Økland et al. 2004; Wild et al. 2004; Czerepko 2008). Notably, most previous studies of forest plant community change in Europe were based on permanent relevé networks placed in even-aged stands (Falkengren-Grerup 1986; Thimonier et al. 1994; Økland et al. 2004). In even-aged stands, changes in understorey vegetation may mainly reflect internal processes of stand development and management practices (Thimonier et al. 1994). Consequently, warming-driven impacts on long-term floristic changes within even-aged stands are likely to be difficult to disentangle from changes driven by stand development and management. In uneven-aged stands, management practices have a lesser impact on stand characteristics over time, and stand structure is likely to be at a dynamic equilibrium (O'Hara et al. 2007), smoothing any stand dynamics-related effects that might otherwise mask or modify the potential plant community response to climatic warming.

We hypothesize that recent changes in plant community composition, that are likely caused by warmer temperature conditions, might result in an increasing proportion of thermophilic species not only in even-aged stands but also in uneven-aged stands. At the species distribution level, we expect lowland species to increase in frequency and expand at their higher altitudinal range margins, whereas we expect mountain species to decrease in frequency and contract at their lower altitudinal range mar-

gins. Here, we assessed changes in plant community composition within both even- and uneven-aged stands in temperate mountain forests by re-surveying 154 *Abies alba* forest vegetation relevés, at mid-elevations (550–1,350 m a.s.l.) in the Jura Mountains (France and Switzerland). Surveys were conducted in 1989 (Bert 1992a) and repeated in 2007, and thus our study covers much of the period of rapid warming and unprecedented (on a 1000-year time scale) high global mean temperatures during the last 20 years (Moisselin et al. 2002; Rebetez & Reinhard 2008). We used permanent relevés within mature forest stands to ensure that any changes observed were not driven by land-use change (Sala et al. 2000). It is also clear that nitrogen deposition increased in this part of Western Europe in the past (Holland et al. 2005), and we therefore carried out soil comparison analyses between the 1989 and 2007 data to test for soil chemical changes that could also affect plant community composition.

Methods

Study area

The Jura Mountains lie on the border between France and Switzerland (Fig. 1). This mountain range is a relatively homogeneous calcareous massif, with soil types including rendzinas, humic cambisols, chromic cambisols, orthic luvisols and chromic luvisols (FAO 1988). The study area spans 550–1,350 m a.s.l., and mean annual temperature and precipitation during the 1965–2007 period ranged from 10.6°C and 1,150 mm yr⁻¹ at the Besançon meteorological station (307 m a.s.l., Météo-France) to 5.8°C and 2,050 mm yr⁻¹ at the Lamoura meteorological station (1,120 m a.s.l., Météo-France), respectively. Using data from 13 meteorological stations situated at 236 to 1,120 m a.s.l. within the study area, we found that mean annual temperature increased by 1.3°C in eastern France (Fig. 2a) and 1.1°C in western Switzerland (Fig. 2c) between the periods 1979–1988 and 1997–2006. From 1965 to 2007, rainfall did not exhibit any clear trend in this region (Fig. 2b, d).

The forest area is managed as regular (even-aged stands) and plenter (uneven-aged stands) systems; the latter being a common practice in the Swiss part of the mountain range. At present, most even-aged stands are progressively being converted into uneven-aged stands both in France and Switzerland. The forest stands were pure silver fir (*Abies alba* Mill.), mixed silver fir/Norway spruce (*Picea abies*

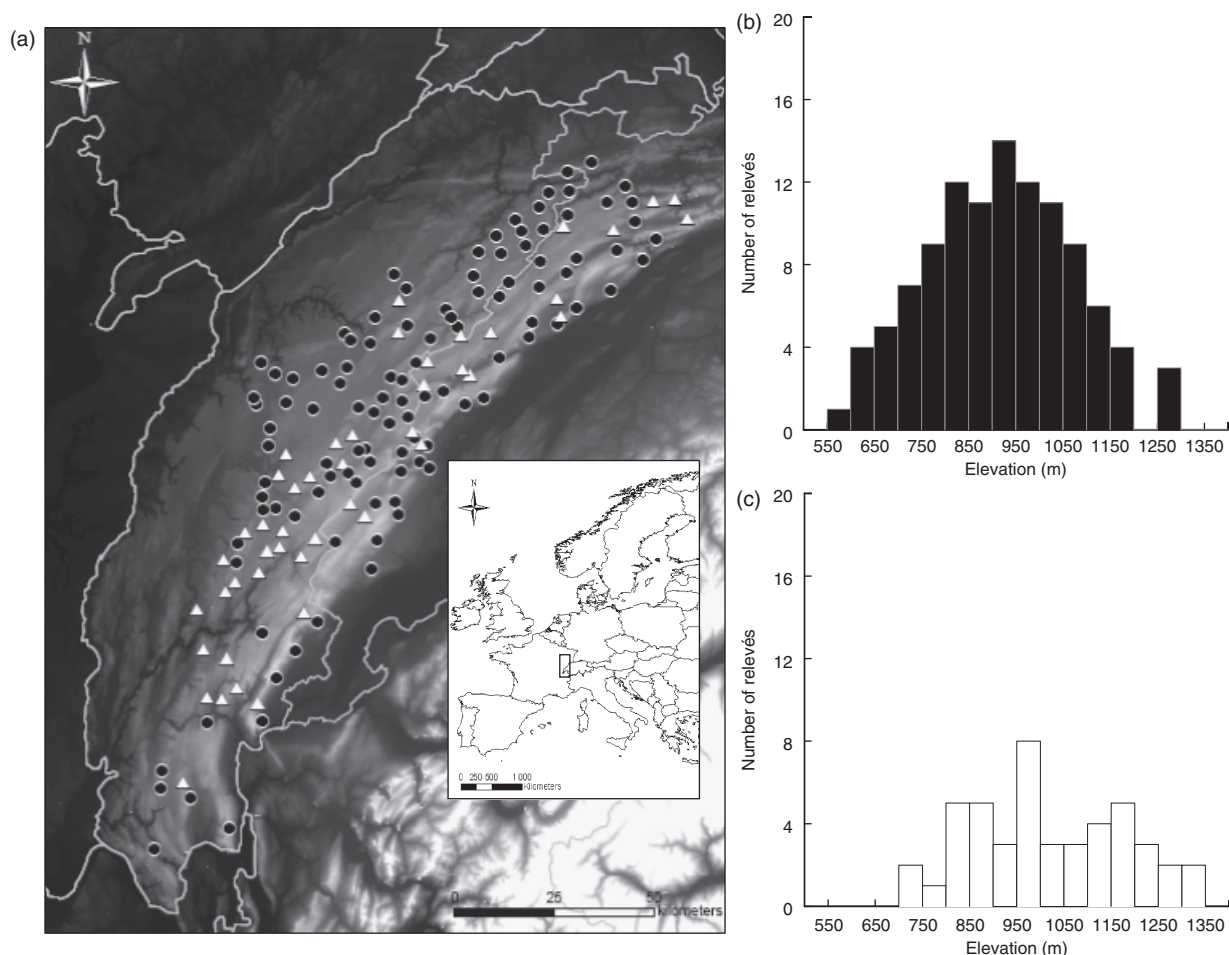


Fig. 1. Location of the 154 re-surveyed forest relevés in (a) the Jura Mountains on the border of France and Switzerland, and altitudinal distribution of relevés in (b) even- ($n = 108$) and (c) uneven-aged stands ($n = 46$). Black dots and black histogram bars represent relevés in even-aged stands whereas white triangles and white histogram bars represent relevés in uneven-aged stands.

L. Karst.), silver fir/European beech (*Fagus sylvatica* L.) or silver fir/Norway spruce/European beech (Bert 1992a).

Initial sampling set-up in 1989

The initial sampling was conducted by Bert (1992a) from May to October 1989 and was aimed at assessing the impact of ecological factors, climatic stresses and pollution on the growth and health of *A. alba* in the Jura Mountains. It comprised 208 relevés (144 in France and 64 in Switzerland) that were representative of the natural range of *A. alba* in the Jura Mountains (Bert 1992b). The sample density was, on average, one sample per 800 ha of *A. alba* forest. Only *A. alba* stands (>50% *A. alba*) were included in the survey, with 54 relevés in uneven-aged plenter forest stands and 154 relevés in even-aged regular forest stands. The size of the original

relevés was about 250 m², without strong variations in soil and topographic conditions (Bert 1992a).

Complete vascular plant species lists were recorded on each site. However, trees > 8 m in height were not included in the analyses of the present study, as they would mostly reflect forest management. Indeed, by including mature trees in the analyses, we might introduce changes in composition that are only due to silvicultural decisions during thinning operations (e.g. elimination of spruce to the benefit of fir or beech).

In addition, a number of geographic environmental factors describing meso- and topo-climatic conditions were also recorded for each site: latitude (YSN expressed in decimal degrees, in the WGS84 system), longitude (XWE expressed in decimal degrees, in the WGS84 system), altitude (ALT expressed in meters), slope (SLO expressed as percentage) and aspect (A expressed in degrees,

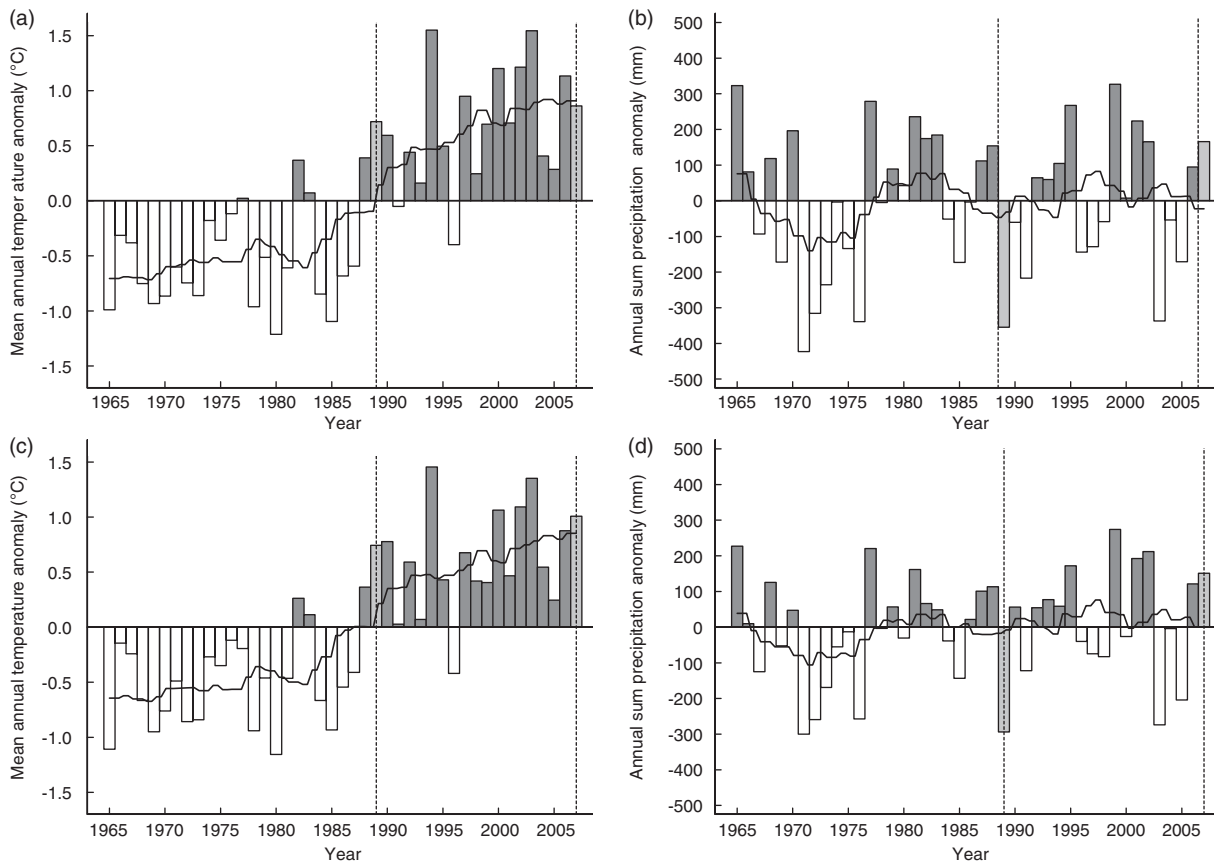


Fig. 2. Trends in mean annual temperature and precipitation from 1965 to 2007 in (a, b) eastern France and (c, d) western Switzerland: (a, c) Yearly mean surface temperature anomalies (overall mean of temperature as baseline) and (b, d) annual sum of precipitation anomalies (overall mean of annual sum of precipitation as baseline) averaged for (a, b) 10 elevation sites (ranging from 236 to 1,120 m a.s.l.) in the French part of the Jura range and for (c, d) three elevation sites (ranging from 316 m to 1,073 m a.s.l.) in the Swiss part of the Jura range. Filled dark grey bars are positive anomalies, whereas empty bars are negative anomalies. Filled light grey bars are 1989 and 2007 sampling times. The dark curves have been smoothed using a 10-year filter. Data were gathered from the French National Climatic Network (Météo-France) and the Swiss Climatic Network (Météo-Suisse).

counter-clockwise from north). Because aspect is a circular predictor variable, we used cosine and sine transformations to avoid modelling issues. The cosine of aspect (northness, ASN) represents the orientation in the south–north direction, whereas the sine of aspect (eastness, AWE) represents the orientation in the west–east direction. A soil pit was dug to describe the soil profile and record soil depth (DEP expressed in centimeters). SLO and DEP were included in the analyses as water-related variables because Bert (1992b) found that water availability is the second major driver of variability in plant community composition, in addition to temperature (here, represented by altitude). An initial assessment of soil from each of the 208 relevés was conducted by Bert (1992a), and he selected 23 samples that represented a broad range of soil types and conditions found throughout the study area. In each of these

selected relevés, Bert (1992a) collected A-horizon soil samples, which were then air-dried and sieved at 2 mm. Then soil pH-H₂O was measured with pH electrodes after 1/5 dilution of fine earth. Total nitrogen and organic carbon were also measured using the Kjeldahl and Anne methods (Bert 1992a), respectively.

During 1989, the growing season (May–October) was particularly dry: the average temperature was 15°C and cumulative precipitation was just 384 mm in both eastern France and western Switzerland (Météo-France, Météo-Suisse).

2007 re-survey sampling design

From May to October 2007, we re-surveyed 154 of the relevés established in 1989: 46 in uneven-aged stands and 108 in even-aged stands (Fig. 1). Figure 1

also provides details on the altitudinal distribution of these relevés. The remaining 54 relevés were also re-located but were not re-surveyed because they were highly disturbed by heavy thinning, clear-cutting or by a severe storm in 1999. Initial relevé relocation in 2007 was done using a handheld Global Positioning System (GPS) and coordinates from 1989 maps of relevé positions. Paint marks and label numbers placed on six *A. alba* trees per relevé in 1989 were still recognisable on trees that remained in 2007, thereby enabling highly precise re-location of relevés.

We identified all vascular plant species within a rectangular surface area of 250 m² around the centre of each relocated relevé. Species nomenclature followed Flora Europaea (Tutin et al. 2001), and identification errors were reduced by aggregating easily confused, closely related species (e.g. *Bromus benekenii* and *Bromus ramosus*) into a single taxon. During the re-surveying, the recording sequence for each species was noted. Two observers in 2007 spent the first inventory week with two of the 1989 observers so as to calibrate themselves to the 1989 sampling methodology. However, the two observers in 2007 spent much more time sampling than the two 1989 observers. Each relevé was sampled for at least 1 h so as to be as exhaustive as possible (Archaux et al. 2006). Plant census differences can strongly influence relevé species richness (Archaux et al. 2009). Notably, re-surveying of old relevés that were not initially intended to be re-surveyed often show an increase in species richness over time that reflects the more exhaustive sampling used during the re-survey (Archaux et al. 2009). In all our comparative analyses, we focused on species composition, not on species richness, and accounted for the potential effect of the increased exhaustiveness of the 2007 census by running analyses on two complementary data sets: (i) the complete species lists from 1989 and 2007 and (ii) the complete 1989 lists but truncating the 2007 list per relevé to the same number of species as in 1989 (n_{1989}) using only the first recorded n_{1989} species from the 2007 list (except that shrubs, i.e. woody plants of higher stature than herbs and ferns, were never excluded given their higher visibility). Analysis of these two complementary data sets represented the opposite extremes in terms of attributing richness increases between 1989 and 2007 as either completely real (the complete data set) or completely due to greater sampling exhaustiveness in 2007 (the truncated data set), with the actual situation likely to lie somewhere between the two. The data truncation probably provides the most valid results, since herbs and ferns

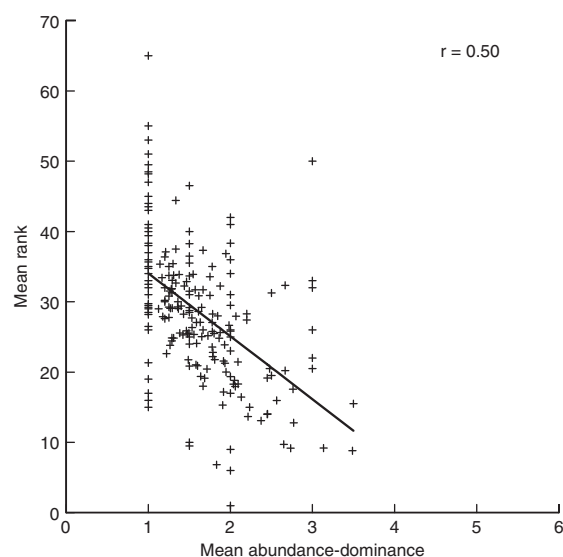


Fig. 3. Relationship between species mean abundance–dominance in a relevé (cover abundance scale ranging from 1 to 6) (Braun-Blanquet 1932) and species mean rank of their recording sequence in a relevé in 2007. Each cross represents a species. Average values are computed for herb and fern species only and for the 154 re-surveyed relevés only.

recorded late in the sequence in 2007 were generally rare and among the least detectable species inside the relevés (Fig. 3).

Geographical (YSN and XWE) and environmental (ALT, ASN, AWE, SLO, and DEP) characteristics in 1989 and 2007 were identical because of the precise re-location of plots. Among the 23 relevés selected for soil analyses in 1989, we were able to re-survey 18 using the same methodology.

During the growing season of 2007, the average temperature (14.5°C) was slightly lower than in 1989, despite the overall warming trend, whereas cumulative precipitation (840 mm) was much higher (Météo-France, Météo-Suisse).

Multivariate analysis: assessing changes in vegetation composition between 1989 and 2007

First, we carried out a correspondence analysis (CA) (Jongman et al. 1987) on the 1989 species lists (presence–absence) of the 154 re-surveyed relevés (CA₈₉) to determine the major gradients driving species composition in these *A. alba* stands. Herbs, ferns and shrubs were analysed together. Rare species (frequency < 5 occurrences in the 154 relevés) were included in the analyses only as supplementary variables. In total, 135 species were retained as active for CA₈₉. To explain the variation accounted for by the first two ordination axes of CA₈₉, ordin-

ary least squares (OLS) partial regression was then used to partition the variation in the first and second CA₈₉ axes into the component purely explained by environmental variables (ALT, ASN, AWE, SLO and DEP), the component purely explained by geographical variables (YSN and XWE) and a mixed environmental–spatial component jointly explained by the two sets of explanatory variables (Legendre & Legendre 1998). We tested for correlations among the first two CA₈₉ axes and the environmental variables using Dutilleul's correction for spatial autocorrelation, and also tested for spatial autocorrelation in the residuals of the OLS models with all seven predictors using Moran's I (estimated for 14 distance classes). These regression and spatial analyses were computed using Spatial Analysis in Macroecology (SAM), version 3 (Rangel et al. 2006). To ensure that our results were robust, we also ran the analyses using principal component analysis (PCA) after applying the Hellinger distance transformation to the species data, which is an ordination approach recommended by Legendre & Gallagher (2001). This transformation allows species distribution data with many zeroes and non-linear species response curves to be analysed by Euclidian-based ordination methods like PCA, thereby offering an alternative to the chi-square distance-based CA and its derivatives (Legendre & Gallagher 2001).

Second, CA₈₉ was implemented with the 1989 relevés as active and the 2007 relevés as supplementary to analyse shifts in relevé position from 1989 to 2007 with 1989 as reference. Each relevé was characterized by its 1989 and 2007 position on the first two CA₈₉ axes. The shifts of the relevés in their 1989 and 2007 positions on the first two CA₈₉ axes were used to indicate changes in site conditions for even- and uneven-aged stands. The statistical significance of these shifts was tested using Student's paired sample *t*-tests.

Indicator value analysis and soil analyses: testing for changes in environmental conditions between 1989 and 2007

We applied Landolt's indicator system (Landolt 1977) to estimate environmental conditions at each forest site and analyse differences in environmental conditions between 1989 and 2007 for both even- and uneven-aged stands. Landolt (1977) ranked the vascular plant species of Central Europe according to their occurrence optimum along key environmental niche axes for plants (L: light; T: temperature; K: continentality; F: soil moisture; R:

soil pH; and N: soil fertility) using ordinal scales (ranging from 1 to 5). Landolt's values were calibrated in Switzerland and therefore were better suited to our study area than the similar, but better known, Ellenberg's indicator system (Ellenberg et al. 1992). To estimate the value of an environmental factor for a relevé, a weighted average was calculated by averaging all indicator values for one factor for those vascular plant species present in the relevé (disregarding absent taxa and those lacking indicator values). We also analysed differences in C/N ratio and soil pH between 1989 and 2007. The statistical significance of these differences in environmental conditions between 1989 and 2007 was tested using Student's paired sample *t*-tests or Wilcoxon signed-rank tests depending on the normality of the distribution.

Presence records analysis: detecting distribution shifts

To understand changes in plant community composition between 1989 and 2007, we analysed each species frequency and altitudinal distribution, focusing on herbs, ferns and shrubs commonly found in *A. alba* stands (i.e. present at least ten times in 1989 and 2007). We distinguished mountain and lowland species using distribution maps available in the Flore Forestière Française (Rameau et al. 1989, 1993). Mountain species were those mostly restricted to mountain ranges and their vicinity (Rameau et al. 1989), whereas lowland species were those mostly distributed in plains and at lower elevations below the montane vegetation belt (Rameau et al. 1993). To validate the use of these two geographic species groups, we also tested for differences in habitat conditions between mountain and lowland species by computing mean Landolt indicator values in both groups and using a Student's two-sample *t*-test. Species were then ranked in each group according to their percentage change in frequency.

To highlight differences in species distribution between 1989 and 2007, for each mountain and lowland species we selected all 1989 and 2007 relevés with presence values. We then sorted them by altitudinal location and computed the nine altitudinal values that divide this frequency distribution into ten groups of equal frequency (deciles). Finally, we computed differences between 1989 and 2007 for the 1st, 5th and 9th deciles of each species to assess changes at the lowest, central and highest position of their altitudinal range, respectively. The statistical significance of the mean difference for the 1st, 5th

and 9th deciles was tested using Student's paired sample *t*-test. All computations were performed with the S-Plus 2000 Professional Release 3 statistical software (MathSoft Inc., 201 Broadway, Cambridge, MA 02139, USA).

Results

Elevation and water availability gradients

Mountain and subalpine species such as *Adenostyles alliariae*, *Orthilia secunda*, *Ranunculus platanifolius*, *Valeriana montana* and *Veronica urticifolia* were found at the positive end of the first CA₈₉ axis. Lowland species such as *Acer campestre*, *Carpinus betulus*, *Hedera helix*, *Ligustrum vulgare* and *Quercus petraea* occurred at the negative end of this axis. The multiple regression of the first CA₈₉ axis against the seven environmental and geographical variables displayed highly significant positive relationships to both altitude (ALT) and aspect (ASN) (Table 1), implying that upper altitudes and northern exposures share a close floristic composition. Table 1 also shows that the variation was mostly explained by environmental variables and

Table 1. Multiple linear regressions of first and second CA₈₉ axes against topographic-related environmental variables (ALT, altitude in meters; ASN, northness index from -1 to 1; AWE, eastness index from -1 to 1), water availability-related environmental variables (SLO, slope as percentage; DEP, soil depth in centimeters) and geographic variables (XWE, longitudinal position from west to east in decimal degrees; YSN, latitudinal position from south to north in decimal degrees). Standardized regression coefficients and their significance are given. *P* represents probability values for each standardized regression coefficient. Significant coefficients are displayed in bold (at the 0.05 level).

Variables	Axis 1 CA ₈₉		Axis 2 CA ₈₉	
	Coefficient	<i>P</i>	Coefficient	<i>P</i>
ALT	0.875	<10 ⁻⁴	0.04	0.56
ASN	0.188	<10 ⁻³	0.158	0.02
AWE	-0.053	0.29	0.011	0.86
SLO	-0.027	0.58	-0.195	<10 ⁻²
DEP	0.048	0.32	0.173	0.01
XWE	-0.205	0.04	-0.294	0.03
YSN	0.309	<10 ⁻²	0.852	<10 ⁻³
<i>R</i> ²	0.71		0.48	
Purely explained by environmental variables	69%		9%	
Purely explained by geographic variables	2%		33%	
Mixed environmental-geographic	0%		6%	

almost exclusively by altitude. Spatial autocorrelation in the residuals was low ($-0.07 < \text{Moran's } I < 0.05$). Results from the Hellinger distance approach were very similar. Indeed, we found a strong correlation between the first CA₈₉ axis and the first PCA₈₉ axis ($r = 0.97$, *df* Dutilleul's corr. = 54.7, $P < 10^{-3}$).

At the positive end of the second CA₈₉ axis, we found hygrophilic species (*Carex remota*, *Glechoma hederacea*, *Impatiens noli-tangere* and *Lysimachia nemorum*) and drought-sensitive species (*Quercus robur*), whereas relatively drought-tolerant species (*Quercus petraea*) and xerophilic species (*Daphne laureola*, *Laburnum anagyroides*, *Melica nutans* and *Teucrium scorodonia*) were projected onto the negative end. This axis was also significantly related to water availability environmental variables (Table 1): a positive relationship to soil depth (DEP; the deeper the soil, the higher the water availability); a negative relationship to slope (SLO; the steeper the slope, the lower the water availability); and a positive relationship to the northness index (ASN; higher water availability on northern slopes). However, the variation was mostly explained by geographical variables, with latitudinal position (YSN) being highly significant (Table 1). YSN had a positive relationship with the second CA₈₉ axis, while longitudinal position (XWE) had a negative relationship, reflecting a water availability gradient that arises because northern and western Jura slopes receive more precipitation than southern and eastern Jura slopes (Météo-France, Météo-Suisse). Spatial autocorrelation in the residuals was low ($-0.12 < \text{Moran's } I < 0.16$). As for the first CA₈₉ axis, we found a strong correlation between the second CA₈₉ axis and the second PCA₈₉ axis ($r = 0.97$, *df* Dutilleul's corr. = 24, $P < 10^{-3}$).

Shifts along altitudinal and water availability gradients

We found an average downward shift along the first CA₈₉ axis, with most of the relevés displaying a lower coordinate value in 2007 (relevés located below the bisecting line in Fig. 4a and b, i.e. towards a greater frequency of lowland species and/or lesser frequency of mountain species) in both the truncated data set (Fig. 4a) ($\bar{z} = -0.06$, CI [95%] = [-0.08; -0.04], $t = -5.56$, *df* = 153, $P < 10^{-4}$) and the complete data set (Fig. 4b) ($\bar{z} = -0.03$, CI [95%] = [-0.05; -0.01], $t = -3.07$, *df* = 153, $P < 10^{-2}$). In most cases, this trend was still significant when relevés from even- and uneven-aged stands were analysed separately; in the analysis using the complete 2007 species lists in uneven-aged

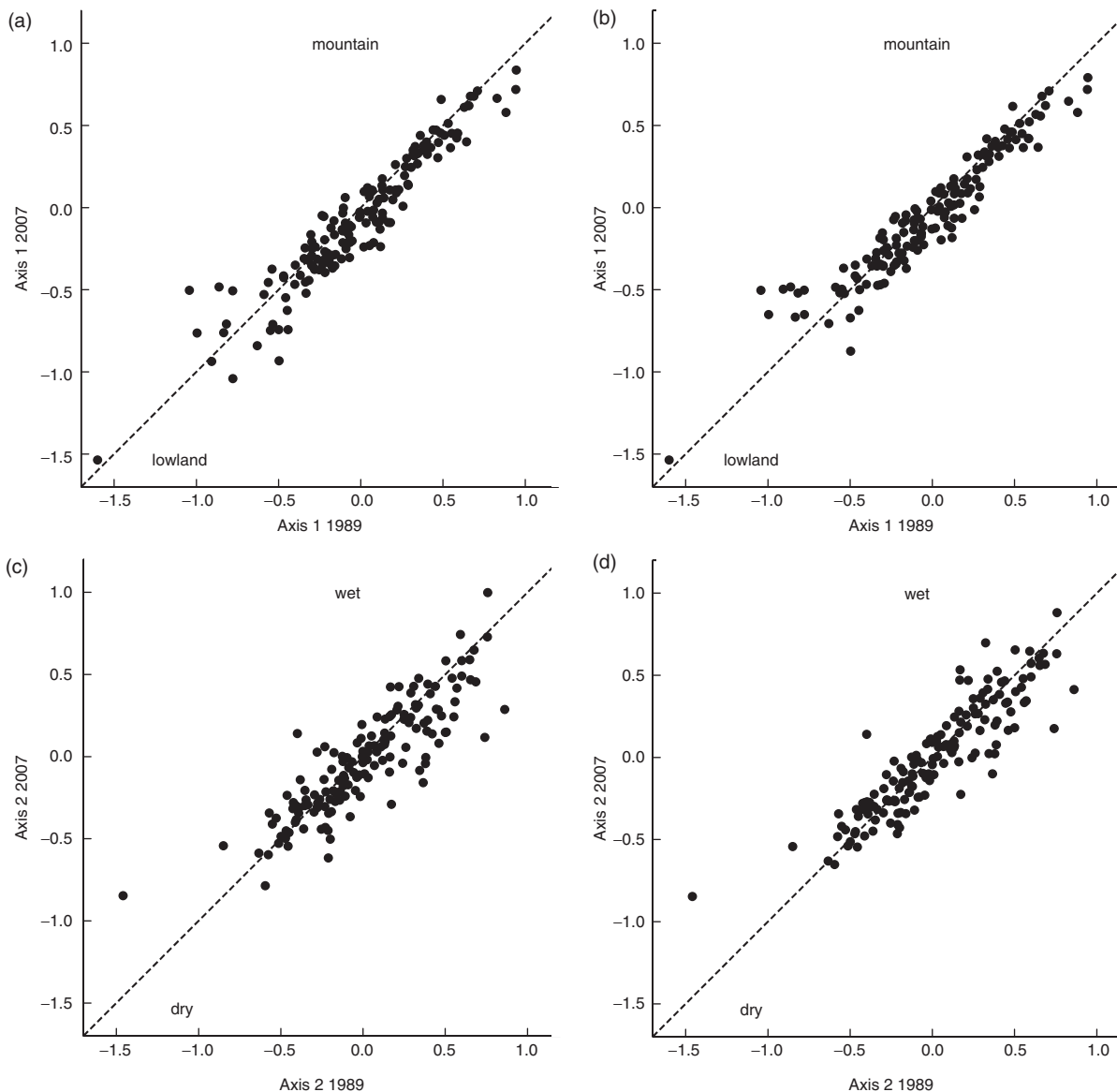


Fig. 4. Scatter diagrams of relevé scores in 1989 and 2007: (a, b) along the first and (c, d) second CA_{89} axes, using both (a, c) the truncated and (b, d) complete 2007 species lists. The first axis corresponds to a gradient of altitude (from lowland to mountain) and the second axis represents a gradient of water availability (from dry to wet). Relevés in 1989 were used as active variables, whereas relevés in 2007 were included in the analyses only as supplementary variables. Dashed bisecting lines represent absence of differences between 1989 and 2007 plot scores (no shift).

stands, the trend was still present but was not significant (Table 2).

There was also an average downward shift along the second CA_{89} axis, with most of the relevés displaying a lower coordinate value in 2007 (relevés located below the bisecting line in Fig. 4c and d, i.e. towards a greater frequency of drought-tolerant species and/or a lesser frequency of hygrophilic species). This shift was significant when using the truncated 2007 species lists (Fig. 4c) ($\bar{z} = -0.04$, CI [95%] = [-0.07; -0.01], $t = -2.64$, $df = 153$,

$P < 10^{-2}$). However, we found no significant trend when using the complete 2007 species lists (Fig. 4d) (CI [95%] = [-0.04; 0.01], $t = -1.08$, $df = 153$, $P = 0.28$). When relevés from even- and uneven-aged stands were analysed separately, the trend was only significant in even-aged stands using the truncated 2007 species lists (Table 2). Figure 4c and d suggest a shift that is not independent of the initial position on the axes. The trend for a downward shift along axis 2 is much clearer at sites with high water availability.

Table 2. Shifts along the first and second CA₈₉ axes between 1989 and 2007 when even- (EAS) and uneven-aged stands (UEAS) are analysed separately using either the truncated or the complete 2007 species lists. *P* represents probability values from Student's paired sample *t*-tests between values in 1989 and 2007. Significant shifts are displayed in bold (at the 0.05 level).

Stand dynamics	Truncated				Complete			
	Axis 1		Axis 2		Axis 1		Axis 2	
	Shift	<i>P</i>	Shift	<i>P</i>	Shift	<i>P</i>	Shift	<i>P</i>
UEAS	-0.058	0.01	-0.008	0.72	-0.044	0.06	0.016	0.38
EAS	-0.061	<10 ⁻⁴	-0.053	0.01	-0.029	0.02	-0.028	0.11

Table 3. Means of Landolt's indicator values for light (L), temperature (T), continentality (K), humidity (F), pH (R) and nitrogen (N) in even- (EAS) and uneven-aged stands (UEAS) using both the truncated and the complete 2007 species lists. 2007–1989 represents the differences between the means in 1989 and 2007. *P* represents probability values from Student's paired sample *t*-tests between values in 1989 and 2007. Statistically significant differences are displayed in bold (at the 0.05 level). Note that *P* values were not adjusted for multiple tests.

Time	L		T		K		F		R		N	
	UEAS	EAS	UEAS	EAS	UEAS	EAS	UEAS	EAS	UEAS	EAS	UEAS	EAS
Truncated												
1989	2.217	2.170	3.023	3.098	2.652	2.595	2.989	3.039	3.059	3.080	3.002	3.060
2007	2.228	2.197	3.049	3.122	2.648	2.601	2.985	3.031	3.064	3.088	2.983	3.051
2007–1989	0.012	0.027	0.026	0.023	-0.004	0.006	-0.004	-0.008	0.006	0.008	-0.020	-0.008
<i>P</i>	0.41	0.01	0.01	<10 ⁻²	0.69	0.31	0.62	0.19	0.54	0.24	0.11	0.32
Complete												
1989	2.217	2.170	3.023	3.098	2.652	2.595	2.989	3.039	3.059	3.080	3.002	3.060
2007	2.243	2.222	3.049	3.125	2.643	2.604	2.991	3.039	3.060	3.076	2.986	3.065
2007–1989	0.026	0.052	0.026	0.027	-0.009	0.009	0.001	0.001	0.001	-0.004	-0.017	0.005
<i>P</i>	0.07	<10 ⁻⁴	<10 ⁻²	<10 ⁻³	0.31	0.14	0.85	0.93	0.91	0.57	0.15	0.55

Changes in environmental conditions

The 46 relevés in uneven-aged stands showed a significant increase of Landolt's temperature (*T*) values between 1989 and 2007 (Table 3), i.e. plant composition during this time changed over time such that it included an increased proportion of thermophilic species in 2007. This change was significant and of similar magnitude irrespective of whether the truncated or complete 2007 species list was used in each relevé (Table 3).

For the 108 relevés in even-aged stands, both Landolt's light (*L*) and *T* values increased between 1989 and 2007, i.e. the plant composition during this time changed such that it included an increased proportion of light-demanding and thermophilic species in 2007; again, this was irrespective of whether the truncated or the complete 2007 species list was used in each relevé (Table 3). We also found a positive correlation between changes in *L* and *T* values in even-aged stands in both the truncated ($r = 0.31$, *df* Dutilleul's corr. = 103, $P < 10^{-2}$) and the complete data sets ($r = 0.44$, *df* Dutilleul's corr. = 101, $P < 10^{-3}$).

When focusing solely on relevés with little change in light penetration ($-0.05 < L < 0.05$), there

was still a highly significant increase in *T* values between 1989 and 2007 in both the truncated ($\bar{z} = 0.019$, CI [95%] = [0.004; 0.034], $t = 2.57$, *df* = 53, $P = 0.01$) and complete ($\bar{z} = 0.018$, CI [95%] = [0.005; 0.031], $t = 2.73$, *df* = 48, $P = 0.01$) data sets, even though changes in *L* values were not significant in either case.

For the 18 relevés in which soils were sampled in both 1989 and 2007, we found no significant changes in C/N ratio (CI [95%] = [-1.25; 1.39], $V = 97$, $P = 0.62$) or soil pH (CI [95%] = [-0.23; 0.42], $V = 112$, $P = 0.25$).

Changes in species distribution

We found 31 lowland and 29 mountain species using the Flore Forestière Française (Rameau et al. 1989, 1993). The average Landolt's *T* value for mountain species (2.83) was significantly lower than for lowland species (3.68) ($t = 6.09$, *df* = 58, $P < 10^{-4}$). Most of the lowland species showed increases in recorded presences across the 154 re-surveyed relevés between 1989 and 2007, with more species showing significant increases when using the complete ($n = 10$) as opposed to the truncated

Table 4. Species presence records (i.e., the number of relevés in which the species was recorded) in 1989 and 2007 for mountain and lowland species and changes as a percentage of the total number of relevés ($n = 154$), using either the truncated or the complete 2007 species lists. Pearson's chi-square tests (P .Chi2) for count data indicate significance of changes in species frequencies. Only species with a greater than 5% change are listed. Significant changes are displayed in bold (at the 0.05 level).

	1989	Truncated			Complete		
		2007	Change (%)	P .Chi2	2007	Change (%)	P .Chi2
Lowland species							
Increasing frequency							
<i>Anemone nemorosa</i>	28				41	8.4	0.10
<i>Brachypodium sylvaticum</i>	21	36	9.7	0.04	56	22.7	$< 10^{-2}$
<i>Bromus ramosus</i>	18	29	7.1	0.11	43	16.2	$< 10^{-2}$
<i>Cardamine pratensis</i>	26				35	5.8	0.25
<i>Carex flacca</i>	27	38	7.1	0.16	59	20.8	$< 10^{-2}$
<i>Carex sylvatica</i>	106	116	6.5	0.25	131	16.23	$< 10^{-2}$
<i>Euphorbia amygdaloides</i>	30	48	11.7	0.03	58	18.2	$< 10^{-2}$
<i>Fraxinus excelsior</i>	92	107	9.7	0.10	107	9.7	0.10
<i>Galeopsis tetrahit</i>	29				38	5.8	0.27
<i>Hypericum hirsutum</i>	16				36	12.9	$< 10^{-2}$
<i>Luzula pilosa</i>	33				49	10.4	0.05
<i>Melica uniflora</i>	33				42	5.8	0.29
<i>Potentilla sterilis</i>	12				24	7.8	0.05
<i>Primula elatior</i>	62				78	10.4	0.09
<i>Quercus petraea</i>	13	31	11.7	0.01	31	11.7	0.01
<i>Stachys sylvatica</i>	20				45	16.2	$< 10^{-2}$
<i>Viburnum opulus</i>	21	29	5.2	0.28	29	5.2	0.28
Decreasing frequency							
<i>Solidago virgaurea</i>	48	38	-6.5	0.25	38	-6.5	0.25
Mountain species							
Increasing frequency							
<i>Cardamine heptaphylla</i>	65				75	6.5	0.30
<i>Festuca altissima</i>	70				80	6.5	0.30
<i>Hordelymus europaeus</i>	99				119	12.9	0.02
<i>Knautia dipsacifolia</i>	38				51	8.4	0.13
<i>Moehringia muscosa</i>	20				28	5.2	0.27
<i>Sorbus mougeotii</i>	25	35	6.5	0.20	35	6.5	0.20
Decreasing frequency							
<i>Lathyrus vernus</i>	88	69	-12.3	0.04			
<i>Orthilia secunda</i>	30	22	-5.2	0.29			
<i>Prenanthes purpurea</i>	101	93	-5.2	0.41			
<i>Senecio ovatus subsp. ovatus</i>	49	41	-5.2	0.38			

($n = 3$) 2007 species list (Table 4). Table 4 also shows that only *Solidago virgaurea* decreased in recorded presence, though not significantly, and that *Brachypodium sylvaticum*, *Euphorbia amygdaloides* and *Quercus petraea* showed significant increases in recorded presences in both truncated and complete data sets. Few mountain species showed changes in recorded presence; some decreased when using the truncated 2007 species list in each relevé and others increased when using the complete 2007 species list in each relevé (Table 4). Only one mountain species showed significant changes in recorded presence between 1989 and 2007, regardless of whether the truncated or complete 2007 species list in each relevé was used in the analysis.

Regarding changes in species altitudinal range at the 1st, 5th, and 9th deciles between 1989 and 2007, we found no shifts for lowland species when using the truncated 2007 species list in each relevé

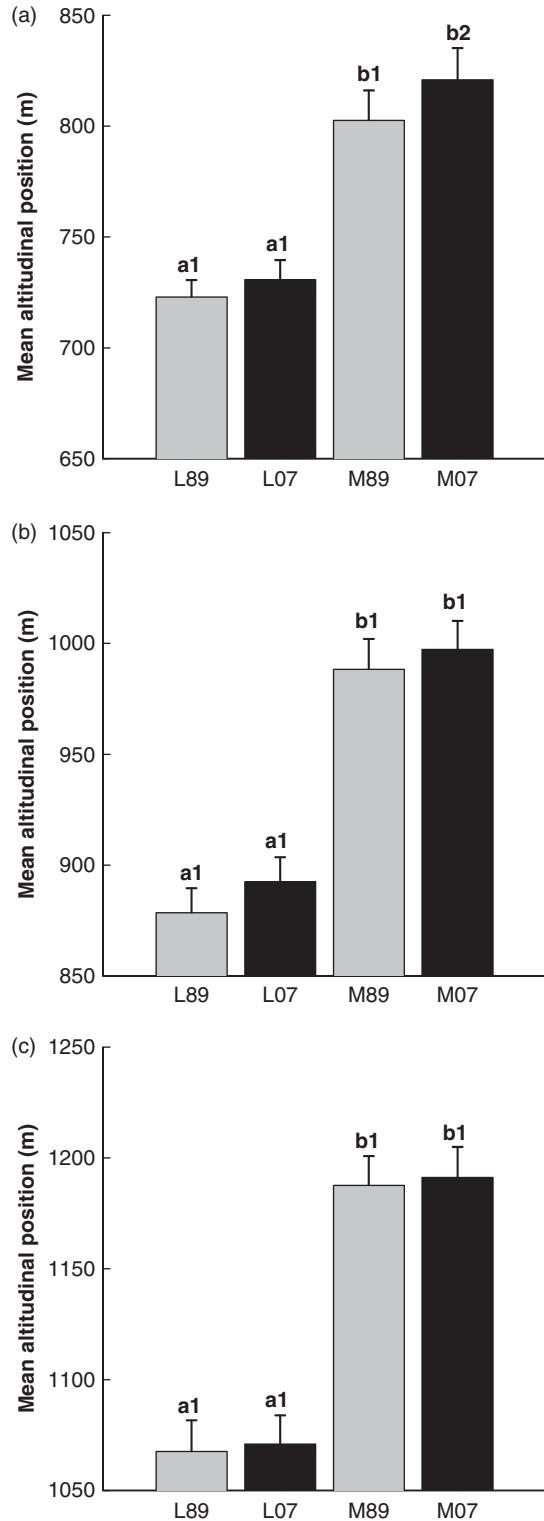
(Fig. 5). Similar results were found when using the complete 2007 species list in each relevé. The 1st decile of mountain species rose by ~ 18 m between 1989 and 2007 (CI [95%] = [0.81; 35.71], $t = 2.14$, $df = 28$, $P = 0.04$) when using the truncated data set (Fig. 5a), whereas no shifts were found when using the complete data set.

Discussion

Climate change and plant community composition between 1989 and 2007

We found clear changes in species composition of the understorey vegetation in both even- and uneven-aged *A. alba* stands in the Jura Mountains between 1989 and 2007. Notably, these changes were towards a greater frequency of lowland species

(Tables 2 and 4). As this trend was observed in both even- and uneven-aged stands, it cannot be attributed to local stand dynamics. Except for mountain species in Table 4, our findings in analyses based on



the truncated and complete data sets were similar, and therefore robust to potential differences in sampling exhaustiveness between the two years (Table 2). This is consistent with expected plant community adjustment to climate warming, and is similar to that previously reported for alpine and nival elevation zones (Klanderud & Birks 2003; Lesica & McCune 2004; Pauli et al. 2007; Erschbamer et al. 2009; Wilson & Nilsson 2009). Our study is one of the few that have focused on sites below the tree line, where other authors previously found low impacts of climate change (Vittoz et al. 2009) or only a slight tendency towards increasing dominance of thermophilic species (Walther & Grundmann 2001).

According to Landolt's indicator values, we also found a significant increase in thermophilic species in the ground layer vegetation in *A. alba* stands for both the truncated and complete data sets. This trend was observed in even- and uneven-aged stands and hence cannot be attributed to local stand dynamics (Table 3). The trend coincided with a prolonged period of climatic warming: mean annual temperatures increased by $\sim 1.0^{\circ}\text{C}$ in the study area from 236 to 1,120 m a.s.l. between 1979-1988 and 1997-2006. However, Table 3 also shows that in even-aged stands, ground layer vegetation exhibited an increase in light-demanding species, which probably reflects gap formation from tree thinning and clearing operations in these stands. More light reaching the forest understorey, combined with a warmer microclimate, might explain part of the shift towards the increasing presence of thermophilic species. There was also a significant increase in thermophilic species in uneven-aged stands, but there was no significant increase in light-demanding species; thus, the increase in thermophilic species in uneven-aged stands must largely have another cause. Furthermore, in relevés with little change in light penetration ($-0.05 < L < 0.05$), we still found a significant increase in temperature, as bio-indicated

Fig. 5. Changes in (a) 1st, (b) 5th and (c) 9th decile positions of species altitudinal ranges for both lowland and mountain species between 1989 and 2007, using the truncated 2007 species lists. L₈₉ (grey bars) and L₀₇ (dark bars) refer to lowland species ($n = 31$) in 1989 and 2007, respectively. M₈₉ (grey bars) and M₀₇ (dark bars) refer to mountain species ($n = 29$) in 1989 and 2007, respectively. Means are shown with standard error. Bars not sharing a common letter differ significantly between the two geographic species groups (Student's two-sample *t*-test between lowland and mountain species, $P < 0.05$). Bars not sharing a common number differ significantly between periods (Student's paired sample *t*-test between 1989 and 2007, $P < 0.05$).

by the ground layer vegetation in *A. alba* stands and, again, this pattern was found in both the truncated and complete data sets. Therefore, climate warming appears to be the underlying driver of the increase in thermophilic species in these mid-altitude forests in the Jura Mountains.

When using the truncated 2007 species lists, we also detected changes in plant species composition towards more drought-tolerant species and/or fewer hygrophilic species, especially in even-aged stands (Table 2). Similar shifts towards more drought-tolerant species have been observed in a recent long-term study in forest wetlands in Poland (Czerepko 2008) and in a comparative analysis of changes in species composition of the Central Apennines in Italy (Petriccione 2005). However, this trend was not significant or was even reversed when using the complete 2007 species lists (Table 2). Additionally, we did not find any changes in the presence of hygrophilic species according to Landolt's *F* values in either the truncated or complete data sets. These results do not allow us to reach strong conclusions on the importance of water availability changes to plant community composition, highlighting the need for further studies focusing on both temperature and water availability (Rebetez & Dobbertin 2004).

Climate change and plant species distributions between 1989 and 2007

The species distribution analyses did not indicate major changes in altitudinal distribution of lowland and mountain species, which is contrary to a previous broad-scale study from forests across French mountains that showed an increase in plant species optimum elevation (Lenoir et al. 2008). However, here we found that lowland species mostly increased in frequency at altitudes where they were already present (Table 4) without dispersing upslope (Fig. 5), which is consistent with the *a priori* expectation that increasing temperatures, across their whole range would favour the performance and reproduction of thermophilic species such as *Brachypodium sylvaticum* (<http://sophy.u-3mrs.fr/pltcli/PC7796.html>), *Euphorbia amygdaloides* (<http://sophy.u-3mrs.fr/pltcli/PC2745.html>) and *Quercus petraea* (<http://sophy.u-3mrs.fr/pltcli/PC2856.html>).

When using the truncated 2007 species lists, we found that mountain species went extinct at their lower range margins (mean increase of 18 m from 1989 to 2007) (Fig. 5a), which reflected upslope range contractions. This is consistent with the *a priori* expectation that cold-adapted species such as *Lathyrus*

vernus (<http://sophy.u-3mrs.fr/pltcli/PC4069.html>), which is more abundant in mountainous areas than in other areas in France (Rameau et al. 1993), would suffer from higher temperatures at low elevations. This trend is consistent with previous studies indicating that upslope range contractions are ongoing for plant species at their lower or southern range margins (Zika 1993; Allen & Breshears 1998; Klanderud & Birks 2003; Lesica & McCune 2004; Gworek et al. 2007; Pauli et al. 2007; Lenoir et al. 2009; Wilson & Nilsson 2009), and supports the idea that extinction processes at the rear margin are important in range shift dynamics (Hampe & Petit 2005). However, this trend was not significant when using the complete 2007 species lists. These results do not allow us to make strong conclusions on evidence for shifts in species distribution but rather reflect changes in local frequencies.

Expressed in altitude-related temperature changes, an 18-m difference at the rear margin of a mountain species roughly equates to a temperature difference of 0.1°C, which is much smaller than the observed temperature change of ~1.0°C in the Jura Mountains since 1989 (Fig. 2). The absence of major changes in altitudinal distribution in comparison to the expectation based on the warming climate might reflect one or more of the following: (i) strong dispersal limitation in forest plant species (Svenning & Skov 2007; Svenning et al. 2008), (ii) increased lag time in the population dynamics of many long-lived forest herbs and shrubs relative to the time-scale of this study (Davis 1989), (iii) local adaptation of plant species to new temperature conditions through genetic variability or phenotypic plasticity within populations (Jump & Penuelas 2005), and/or (iv) microclimatic buffering by the tree canopy. Notably, the tree canopy balances weather extremes and therefore has a smoothing effect on inter- and intra-annual variations in temperature.

Other drivers of vegetation changes

Although the observed changes in plant community composition are consistent with the effects of climatic warming, we note that they could also be related to other causes, such as: disturbances (Wild et al. 2004), atmospheric deposition (Thimonier et al. 1994) or game management (Taverna et al. 2005).

Developmental trajectories in forest stands in relation to perturbations, natural ageing and management practices often involve changes in the canopy and contingent changes in light penetration. The latter can be an important ecological driver of long-term changes in forest ground layer vegetation

(Brunet et al. 1997; Nygaard & Odegaard 1999; Wild et al. 2004; Czerepko 2008). In the majority of sites in even-age stands, we found a concomitant increase in Landolt's indicator values for temperature and light, suggesting that at least some of the increase in temperature as bio-indicated by ground layer vegetation might be attributed to changes in light penetration, whether linked to management or natural disturbance.

It has often been suggested that anthropogenic nitrogen (N) deposition has influenced forest plant community composition in Europe (Falkengren-Grerup 1986; Thimonier et al. 1994; Brunet et al. 1998; Økland et al. 2004), either directly by increasing N availability and/or indirectly by accelerating soil acidification (Thimonier et al. 1994; Brunet et al. 1998). Nevertheless, soil chemical analyses from the 18 relevés in which soils were re-sampled suggest a largely stable C/N ratio and pH between 1989 and 2007. We acknowledge that the C/N ratio is not a good or accurate indicator of N deposition because carbon cycling also has a significant impact; however, there were also no trends in Landolt's indicator values for N (Table 3). Hence, there was no indication of an increase in N availability. Concerning soil acidification (Falkengren-Grerup 1986; Økland et al. 2004), the calcareous bedrock of the Jura range is likely to have neutralized any soil acidification processes. Overall, it is thus clear that neither direct nor indirect effects of N deposition explain our results.

Long-term changes in the forest ground layer vegetation have also been related to increases in deer populations (Taverna et al. 2005). Deer populations in Switzerland remained at a steady state between 1985 and 2005 (Office Fédéral de l'Environnement, OFEV sources). In 2005, deer densities in the French mountains were reported to be nine times higher than in 1985 (Pfaff et al. 2008). Nonetheless, this increasing trend depends strongly on region and mostly occurred in the western Alps, northern Pyrenees and the Massif Central, whereas densities in the Jura Department have been decreasing (Pfaff et al. 2008). Hence, there is no indication that overall herbivory pressure in the Jura Mountains changed between 1989 and 2007.

Robustness of changes in plant community composition

Overall, changes in plant community composition between 1989 and 2007 towards a greater frequency of low-altitude, thermophilic species were consistent across the 2007 species lists used for ana-

lysis (truncated or complete). Comparability of historical (1989) and present-day (2007) species lists is particularly important for studies involving different observers over time because changes will often be confounded with differences in observer expertise and/or the nature of the plant censuses (Scott & Hallam 2002; Archaux et al. 2009). Species lists are rarely exhaustive, and overlooked species are common in botanical inventories (Scott & Hallam 2002; Archaux et al. 2006, 2009; Vittoz & Guisan 2007). The majority of overlooked species typically have cover of <0.1% (Vittoz & Guisan 2007); thus, the overlooked species in 1989 are likely to be less frequent within a relevé and are likely to be low-ranked inside this relevé in the 2007 recording sequence (Fig. 3) if their abundances have not increased. Therefore, results from analyses based on the truncated 2007 species lists are probably more representative of real shifts in community composition. However, such species that were rare and overlooked inside a relevé in 1989 might also have increased in cover and become more abundant in this relevé by 2007; then they would be likely ranked higher in the recording sequence (Fig. 3). In this case, the truncation approach would still be representative of real shifts because the estimates of community composition would emphasize the more common species in both years, and estimates of changes would represent shifts from rare/absent to abundant or vice versa. However, by running all analyses using the truncated and complete 2007 species lists we were able to assess the robustness of our findings, as the true situation is likely to lie somewhere between (arguably closest to truncation-based results). As the results were largely consistent between the two approaches, we conclude that our results are robust.

Conclusion

Mean annual temperature in the Jura Mountains has increased by $\sim 1.0^{\circ}\text{C}$ between 1989 and 2007. While the descriptive nature of the present study precludes rigorous inference regarding climatic warming effects on plant community composition in the region, we found vegetation changes between 1989 and 2007 that were clearly consistent with climate warming. Notably, there was a significant shift towards a greater frequency of low-altitude, thermophilic species. This shift was consistent across stand types, and therefore cannot be attributed exclusively to local stand dynamics. However, part of this shift in even-aged stands was

attributed to a concomitant increase in temperature and light, as bio-indicated by ground layer vegetation, suggesting the influence of stand dynamics-related effects. The observed changes largely reflect changes in local frequencies rather than major changes in altitudinal distributions, although it appears that the lower altitudinal range margins of some mountain species might have contracted upslope. We conclude that in the Jura Mountains, forest plant community composition is now not only driven by local stand dynamics; but that the communities are also facing broad directional changes that are likely driven by climate change. Hence, recent warming is now driving plant community change not just in the climatically extreme arctic and alpine ecosystems but also in more moderate situations.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Photo S1. A silver fir trunk with paint mark and label number from 1989 indicates the location of one of the 154 re-surveyed relevés in the Jura Mountains in summer 2007.

Photo S2. A re-surveyed relevé located in an even-aged stand dominated by mature silver fir in the Jura Mountains, summer 2007.

Photo S3. A re-surveyed relevé located in an uneven-aged stand dominated by silver fir at different life stages in the Jura Mountains, summer 2007.

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